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THE PHYTOPLANKTON OF SUDBURY AREA LAKES (ONTARIO) AND THE RELATIONSHIPS WITH ACIDIFICATION STATUS

MARCH 1992

Ontario
Environment
Environnement

ISBN 0-7729-9424-2

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and
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MARCH 1992

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AND

THE RELATIONSHIPS WITH ACIDIFICATION STATUS

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ABSTRACT

Nicholls, K.H., L. Nakamoto and W. Keller. 1992. The phytoplankton of Sudbury area lakes (Ontario) and the relationships with acidification status. Can. J. Fish. Aquat. Sci. (in press).

Phytoplankton data from samples collected in July, 1981 from 111 lakes in the Sudbury area were analyzed by canonical community ordination analysis (CCA) and other techniques to reveal associations of taxa which were related to environmental gradients among the lakes. Phytoplankton data from a group of seven lakes sampled in the mid-1970s or early 1980s and in the mid-1980s were analyzed for evidence of temporal change. In both data sets factors related to trophic status and acidification status were inferred to be important controlling variables. For example, desmid genera fell into two general groupings, one typical of clear water, nutrient-poor, low alkalinity lakes (e.g., species of *Micrasterias, Bambusina, Euastrum, Spondylosium*), the other representing lakes higher in nutrients and alkalinity (e.g., species of *Teilingia, Closterium, Xanthidium, Staurastrum*). This latter group also included several chlorophytes (*Ulothrix, Schroederia, Scenedesmus*) and euglenoids (*Euglena, Phacus*). Well defined relationships existed between lake alkalinity, pH and total numbers of phytoplankton taxa. The smaller data set included lakes subjected to recent decreases in acid deposition and corresponding increases in pH over a 10 year interval, and the increased numbers of phytoplankton taxa were indicative of recovery from earlier acidification.

Key Words: phytoplankton, acidification, lakes

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INTRODUCTION

Since the recognition of anthropogenic acid deposition as a major impact on lake ecosystems in Scandinavia and northeastern North America, acidification effects on phytoplankton have been examined in laboratory simulations, experimental enclosures, comparative lake studies, synoptic multi-lake surveys and long term whole-lake acidification and neutralization experiments [see reviews by Stokes (1986), Geelen and Leuven (1986) and Weatherley (1988)]. The earliest results were somewhat inconclusive with respect to certain effects on phytoplankton (e.g., whether or not production and biomass were influenced by acidification). Recent data clearly demonstrate that phytoplankton production and biomass are controlled by the supply of limiting nutrients (Havens and DeCosta 1984; Kerekes et al. 1990). Factors such as metal toxicity, especially Al (Paul and Nalewajko 1984; Havens and DeCosta 1987; Pillsbury and Kingston 1990), zooplankton grazing (McCauley and Briand 1979) and competition for low levels of dissolved inorganic carbon (Williams and Turpin 1987) act indirectly and variably to control biomass and composition of the phytoplankton of acidic lakes. Loss of species from the phytoplankton is a major effect of lake acidification (see reviews by Geelen and Leuven 1986; Stokes 1986; Minns et al. 1990).

The Sudbury area of central Ontario includes many lakes which have been impacted by acidic deposition from metal smelting operations. The phytoplankton of some of these lakes has been studied over a number of years (Yan 1979; Yan and Miller 1984). The studies include observations of changes induced by whole-lake neutralization with base additions (Yan and Dillon 1984; Molot et al. 1990). Recent reductions in sulphur dioxide emissions from the Sudbury smelters have been related to increases in alkalinity and declines in metals (Keller and Pitblado 1986; Dillon et al. 1986; Hutchinson and Havas 1986), recovery of planktonic rotifer and crustacean populations (MacIsaac et al. 1986; Keller and Yan 1991), as well as recovery of other biota of Sudbury area lakes (Keller et al. 1992). There have been no previously published synoptic phytoplankton surveys of Sudbury area lakes. The only evidence so far for recovery of phytoplankton communities in response to $S0_2$ emission decreases is for siliceous algae (diatoms and scaled chrysophytes) for which paleolimnological methods have been used (Dixit et al. 1989).

Phytoplankton samples were collected from 111 of 250 lakes that constituted part of a large synoptic survey of water quality within a 260 km radius of Sudbury (Pitblado and Keller 1984; Keller and Pitblado 1986). In addition, seven lakes were sampled more intensively (weekly or bimonthly) during the ice-free seasons of 1974 - 1986. Our objectives were to determine:

1) if there were patterns in the phytoplankton communities related to acidification status in the larger lake set, and
2) if significant changes in phytoplankton community structure had occurred in the seven lakes over time.

METHODS

Of the 250 lakes sampled between mid-June and mid-August of 1981, samples for phytoplankton were collected from 111 of these (Fig. 1; Appendix 1) for which visits to lakes could be confined to a short time period in mid-summer (between July 6 and July 21), in order to minimize the effect of seasonality. The locations, morphometric data and watershed characteristics of all lakes were provided in Pitblado and Keller (1984), and for the seven more intensively sampled lakes in Keller and Yan (1991).

Phytoplankton samples from the 111 lakes were collected through the euphotic zone in the deepest part of each lake, using a weighted tygon tube lowered to a depth of 2x the Secchi disc visibility plus one meter. Samples from Whitepine Lake in 1980-81 and Sans Chambre Lake were also collected as non-volume-weighted tygon tube composites. Samples from Whitepine Lake in 1982-86, and Joe and Swan Lakes were collected as euphotic zone composites volume-weighted according to the contribution of different lake strata to the lake volume. Samples from Welcome Lake, Wavy Lake and Laundrie Lake were taken by lowering and raising a weighted sample bottle at a uniform rate through the euphotic zone.

Samples were fixed immediately with Lugol's iodine solution (I-KI-glacial acetic acid), and preserved with formalin after concentration by sedimentation in the Ministry of the Environment's Toronto laboratory.

Phytoplankton analyses on samples collected since 1976 have followed Nicholls and Carney (1979), using inverted microscopy, Utermöhl-type counting chambers, and expression of phytoplankton "density" as cell volume. There was, therefore, consistency in the 111 lake set, but the seven lake data set contained some results (pre 1976) from a very different analytical protocol (compound microscopes with Sedgewick-Rafter chambers). A decision was made to re-analyze the preserved samples in 1986 as pooled composites of the ice-free period. Only a subset of the original 1970s collections were selected for this purpose so that results would be comparable to those from the 1980s when lakes were sampled monthly and samples were also pooled before analyses. This procedure was also intended to remove bias relating to the (presumed) enhancement of analytical expertise over time (potentially important with respect to changes in numbers of taxa over time). Several individual samples (not pooled) from the 1970s collections were re-analyzed in 1986 by the old method (Sedgewick-Rafter cell) to confirm the adequacy of preservation over the approximately 10-year interval. No consistent differences which could be related to a possible preservation problem were found.

Most of the identifications were made to the level of genus (Appendix 2); however, some more easily identified species were recorded (e.g., *Peridinium inconspicuum* (= syn. *P. umbonatum*), *P. limbatum, P. wisconsinense*), while others were grouped at levels above genus (e.g., unidentified "naked" Dinophyceae). Some taxa with suspected autecological differences were also distinguished (e.g., *Chrysochromulina breviturrita* and *C. parva*). Taxa were grouped under seven classes and compiled in ASCII format for PC use with statistical and plotting programmes (SYSTAT v. 4.0 and 5.0; CANOCO v. 2.1 (ter Braak 1988); Freelance v. 3.01).

Multivariate community analyses techniques based on older methods such as multiple linear regression models are often inadequate to define species - environmental variable relationships because these models assume linear relationships, which in reality are more likely to be unimodal (ter Braak and van Dam 1989). Canonical correspondence analysis (CCA; applied with the computer programme "CANOCO"; ter Braak 1988) is a unimodal statistical model which has clear advantages over other multivariate analysis techniques (ter Braak and van Dam 1989). It was used here to identify the relative positioning of assemblages of phytoplankton taxa along environmental gradients in the CCA ordination field. Lakes and phytoplankton taxa were simultaneously ordinated relative to the ordination axes which were constrained to be linear combinations of the environmental variables.

For comparative purposes, and to help in detecting patterns in phytoplankton community composition, a community classification method based on a dendrogram of assemblage dissimilarity values as well as a nonmetric multidimensional scaling ordination ("SYSTAT" statistical software package; Wilkinson 1988) were applied to the species by lake matrix.

Because the input of all taxa from all lakes in multidimensional scaling ordination resulted in an unworkably large data matrix (111 x 121), two separate routines were followed to reduce the data set by about 25%. First, the lakes were arranged in order according to their alkalinity values and every third lake was deleted. The other procedure involved the arbitrary removal of 30 lakes from the middle range of the lake alkalinity/frequency distribution (alk. = 0 - 3.9 mg/L), thus retaining all of the lakes with the lowest and the highest alkalinities for the ordination. In a few cases, where environmental data were not available from the 1981 survey, data from 1982, 1983 or from Regional Ministry of the Environment files for the late 1970s were used. Water chemistry sampling methods have been described by Pitblado and Keller (1984).

RESULTS

A. 111 Lake Set

(i) Chemistry

Of the six major limnological variables considered (alkalinity, dissolved organic carbon (DOC), total phosphorus, total nitrogen, copper, aluminum), only DOC showed a normal distribution among the lakes. The data set included several lakes with high concentrations of copper and aluminum which resulted in skewed frequency distributions of these variables (Fig. 2). In general, the most frequent ranges of chemical variables (representing approximately 70% of all lakes) were: alkalinity, 2 - 4.5 mg/L; dissolved organic carbon, 1.8 - 6.2 mg/L; total phosphorus, 3 - 10 μg/L; total nitrogen, 150 - 350 μg/L; copper, 1 - 2.8 μg/L; aluminum, 15 - 100 μg/L.

(ii) Phytoplankton

Most lakes were low in total biovolume, reflecting their nutrient-poor, oligotrophic status. The most frequent ranges (representing approximately 70% of all lakes) were: total phytoplankton, 0.05 - 0.65 mm^3/L; Bacillariophyceae, 0.05 - 0.2 mm^3/L; Chrysophyceae, 0.01 - 0.09 mm^3/L; Cryptophyceae, 0.005 - 0.06 mm^3/L; Cyanophyceae (non-bloomers), 0.005 - 0.015 mm^3/L; Cyanophyceae (bloomers), < 0.001 - 0.003 mm^3/L; Chlorophyceae, 0.002 - 0.05 mm^3/L (Fig. 3). These data do not include a few "outliers". For example Lake No. 147 (Erables) with 0.148 mm^3/L Cyanophyceae bloomers; Lake No. 16 (Raft) with 0.34 mm^3/L Chlorophyceae; Lake No. 45 (Eagle) with 1.6 mm^3/L Bacillariophyceae and Lakes 54, 143 and 242 (Laura, Klock and Little Laundrie) with 1.31 mm^3/L, 0.47 mm^3/L and 0.53 mm^3/L Dinophyceae, respectively.

Euglenophyceae were poorly represented in the lake set. *Trachelomonas, Euglena* and/or *Phacus* species were recorded from only six lakes. Five of these lakes had relatively high total N and total P levels (301 - 561 μg N/L and 13 - 22 μg P/L), and four were highly coloured (38 - 65 Hazen Units). Dinophyceae were widely distributed (present in 93 of the lakes), but with the few exceptions noted above, biovolumes were very low (< 0.011 mm^3/L in 57% of these lakes). Dinoflagellates were a major part of the total phytoplankton community only in lakes with very low alkalinities (Fig. 4a). The reverse was true for other algal groups and for total phytoplankton biovolume, where positive correlations were observed with lake alkalinity (over the restricted range, - 2 -10 mg/L) and total phosphorus concentrations, but negative correlations were observed with aluminum levels (Table 1).

Total numbers of phytoplankton taxa ranged from lows of 8, 10 and 10 in Lake Nos. 50, 94 and 71 (Chiniguchi, Florence and Nellie Lakes) to a high of 55 in Lake No. 203 (Mowat Lake). The maximum numbers of taxa for the major classes were: 20 Chlorophyceae, 13 Chrysophyceae, 9 Bacillariophyceae, 8 Cyanophyceae, 4 Dinophyceae, 3 Cryptophyceae and 3 Euglenophyceae. Alkalinity, total P and aluminum were the three most important factors related (linearly) to the numbers of phytoplankton taxa (Table 1; Figs. 4b, c). It is clear that the alkalinity/number of taxa relationship is best defined over the low alkalinity range (Fig. 4b). This may also be true of the influence of total phytoplankton biovolume on the total number of taxa, where total biovolumes above 1.0 mm^3/L did not contribute linearly to the relationship (Fig. 4d).

The CCA analysis produced a sample (lake) biplot (Fig. 5), in which the ordination axes were defined by the environmental variables such that each variable was represented by an arrow pointing in the direction of maximum change within the lake set. The longer the arrows, the more highly correlated with the axes are the variables. The most important environmental variables in the 111 lake set (in defining the relative positions of the lakes in the ordination field) were total nitrogen (TN), colour, total phosphorus (TP) and alkalinity. Aluminum and Secchi disc visibility were also important, but were negatively related to the four previously listed variables. This is to be expected both on the basis of intuition (i.e., the most acidic, nutrient-poor lakes are clear-water lakes, highest in aluminum) and on the basis of the linear correlation coefficients (Table 1).

Phytoplankton taxa were ordinated within the same set of environmental axes (Fig. 6) and revealed some interesting relationships. For example, *Peridinium sp*. and *P. limbatum* favoured clearer waters higher in Al and lower in alkalinity than *P. wisconsinense* and *P. inconspicuum*. Virtually all of the bloom-forming, blue-green algal genera (*Aphanizomenon, Microcystis, Gomphosphaeria, Coelosphaerium, Lyngbya, Oscillatoria*) were grouped in the lower left quadrant (Fig. 6), while *Merismopedia, Chroococcus* and *Rhabdoderma* were located in the upper right quadrant (clearer water, higher metals, lower alkalinity, lower nutrients). Several desmid genera (*Micrasterias, Bambusina, Euastrum, Spondylosium*) were all located in the lower right quadrant (clear water, low alkalinity). In contrast, other desmids (*Teilingia, Closterium, Xanthidium*) along with several chlorophytes (*Ulothrix, Schroederia, Scenedesmus*) and euglenophytes (*Euglena* and *Phacus*) clearly favoured lakes higher in nutrients and alkalinity.

Algae associated with high aluminum levels included species of *Tabellaria, Chrysolykos, Mallomonas, Cryptomonas, Chrysochromulina, Rhabdoderma, Paramastix, Chrysosphaerella, Navicula, Asterionella* and *Chrysococcus*. Taxa with a low apparent tolerance for metals (and higher nutrient requirements?) include all of the bloom-forming blue-green algae mentioned above, *Bicosoeca, Trachelomonas, Planctonema, Gomphonema, Stauroneis, Coelastrum, Tetrastrum, Eudorina* and *Dictyosphaerium*. It is noteworthy that the three *Chrysosphaerella* taxa recorded (*C. longispina, C. coronacircumspina* and *Chrysosphaerella sp*. (probably *C. brevispina*) showed a well defined positioning along the Al gradient (Fig. 6). Two colonial chrysophytes recorded as *Uroglena* (No. 48) and *Uroglenopsis* (No. 49), which are likely two (or more) species of the genus *Uroglena*, also showed very different apparent tolerances to aluminum (Fig. 6).

Several well defined groupings of lakes were identified by cluster analyses (Fig. 7) using a measure of dissimilarity of lake phytoplankton communities. For example, lakes with the most dissimilar phytoplankton communities (those clustered near the top of the dendrogram, above "C" in Fig. 7) had, with a few exceptions (Lakes 2, 113, 225 and 54), some of the highest alkalinities in the data set. Also, there were three small sub-sets of lakes, A, B and C (Fig. 7) apparently with relatively similar (within group), but distinctive (between group) phytoplankton communities. Group A lakes were all acidic lakes with negative alkalinities; group B lakes were poorly buffered, but all had alkalinities >0; group C lakes (with the exception of Lake No. 65 with alkalinity = 27.4 mg/L) all had moderately low alkalinities. The average alkalinities of all three groups of lakes (-0.89, 1.25 and 4.7 mg/L, respectively) were all highly significantly different (paired Student's t-tests, $\alpha = 0.001$).

Nonmetric multidimensional scaling (MDS) ordinations were also helpful in identifying gradients among the lakes. Of the two reduced data sets used for MDS, only the set which retained all lakes with extreme alkalinities (see Methods) is illustrated here (Fig. 8), since there were similarities in the two ordinations. Two apparent gradients were identified -one with Lake No. 45 and Lake No. 225 as the end points, and the other with Lake No. 175 and Lake No. 242 as the end points (Fig. 8). Since these were roughly parallel to the first and second ordination axes, respectively, the axis scores for the lakes were regressed against the major environmental variables. Statistically significant correlations ($\alpha = 0.05$) were found for colour and total phosphorus, but not for alkalinity, aluminum or several other variables.

B. The Seven Lake Set

Reliable alkalinity data are not available for the 1970s, but pH data suggest that Welcome Lake had the highest acid neutralizing capacity of the seven lakes and Swan, the lowest (Table 2). Significant increases in pH occurred in all lakes except Welcome Lake and were accompanied by declines in Cu, Ni and Al concentrations (see Table 2 of Keller and Yan, 1991).

Total phytoplankton biovolumes were consistently 2-3 times higher in Swan Lake than in the other six lakes, where biomass ranged approximately between 0.20 and 0.45 mm^3/L (Table 2). In 1976, Laundrie Lake, Stations 2 and 3, had higher biovolumes in the 0.55-0.65 mm^3/L range. No consistent trends over time were observed except in Welcome Lake and Wavy Lake, where mid-1980s biovolumes were considerably higher than in the mid-1970s (Table 2).

At the class level, there were major changes observed over the study period. These included a nearly universal increase in the relative abundance of Chrysophyceae (Fig. 9) and either marked declines in the combined relative abundance of Dinophyceae and Chlorophyceae (as for Swan Lake and Laundrie Lake) or an increase in Dinophyceae and Chlorophyceae, as for Joe Lake and Welcome Lake (Fig. 9). Increases in these classes were at the expense of the Bacillariophyceae.

Total numbers of phytoplankton taxa increased markedly over time in Whitepine, Laundrie, Welcome, Wavy and Joe Lakes (Fig. 10). Swan and Sans Chambre Lakes did not reveal a similar increase, but samples from before 1977 from Swan Lake and 1980 from Sans Chambre Lake were not collected. Total numbers of taxa increased by about 65%, 20% and 65% in Laundrie Lake, Welcome Lake and Joe Lake, respectively. Most of these increases were attributable to species of Chlorophyceae and Chrysophyceae. A highly significant linear correlation (Fig. 11) existed between the total number of phytoplankton taxa recorded and lake pH for the seven lake set (all years).

A detailed evaluation of all taxonomic changes was done for only Joe Lake, Laundrie Lake and Welcome Lake by comparing the changes in abundance of all recorded taxa to the taxon-alkalinity axis of the CANOCO analysis done on the 111 lake set. There do not appear to be simple explanations for the observed changes in phytoplankton. These three lakes showed increased representation by between 21 and 34 taxa and declines in only 1-3 taxa. The inferred controlling influences of alkalinity and several nutrient-related variables could not be separated on the basis of the CANOCO analyses. In Welcome Lake for example, 70% of the taxonomic changes were predictable along the alkalinity and nutrient-related CANOCO axes. Because there was no significant change in the pH of Welcome Lake from the mid-1970s to the mid-1980s, it must be assumed that nutrient-trophic status factors were responsible for these taxonomic changes. Four taxa in the Welcome Lake phytoplankton were not included in this analysis (*Gloeotila, Cryptaulax, Chrysamoeba* and *Chrysidiastrum*) because they were not recorded in the original CANOCO analysis of the 111 lake set. Increases in five other taxa in Welcome Lake (*Chroococcus, Gomphosphaeria, Rhabdoderma, Chrysochromulina parva* and *Chrysosphaerella longispina*) suggested some increased recent influence of aluminum; however, Al concentrations in Welcome Lake did not increase over this period (Keller and Yan 1991).

In Joe Lake, the 1975 phytoplankton was dominated by species of *Dinobryon* and *Asterionella*. These species were much less important in 1985 and 1986 as were species of *Uroglena, Arthrodesmus, Botryococcus*, and *Chrysochromulina brevituritta*. The 1980's community was dominated by the diatoms Cyclotella and *Rhizosolenia* and low densities of many other taxa representing several classes, especially the Chlorophyceae (including desmids) and the Chrysophyceae.

In contrast to Welcome Lake, Joe Lake's aluminum concentrations declined from an average of 70 μg/L in 1975-76 to 19 μg/L in 1985-86 (Keller and Yan 1991). The only taxa showing significant declines in Joe Lake over this time period (*C. breviturrita, Asterionella* and *Dinobryon spp.*) were all closely related to the Al axis of the CANOCO analysis (111 lake set). A total of 34 other taxa showed increased representation. Of these, 75% were consistent with the alkalinity axis of the 111 lake set CANOCO analysis (after omission of seven taxa not included in the CANOCO analysis).

Wavy Lake was the only other lake (in addition to Welcome Lake) where trophic state changes were considered to be more important than changes in acid status. Total phytoplankton biomass increased sharply in 1985 over 1974 levels at all three Wavy Lake stations, then dropped to an intermediate level in 1986 (Table 2). The pH of Wavy Lake held constant at 4.7 in both 1985 and 1986, while the total number of taxa declined from the 1985 high of about 25 taxa to about 22 in 1986 (Fig. 10), thus mirroring the total biovolume changes. The total numbers of phytoplankton taxa in 1974 in Wavy Lake (averaging only about 18 for all three stations) were the lowest recorded numbers of all seven lakes and were consistent with both its extremely low pH (4.7) and its low total phytoplankton biovolume (averaging only 0.06 mm^3/L).

DISCUSSION

Several recent studies have attempted to determine the effects of lake acidification and other factors on phytoplankton by synoptic surveys of large numbers of lakes and associated multivariate analyses of environmental variables (Earle et al. 1986, 1987; Morling and Willén 1990; Pinel-Alloul et al. 1990). Although canonical community ordination analysis is now widely used in paleolimnology for developing relationships between environmental factors and silica-scaled chrysophyte and diatom components in lake sediments (e.g., Dixit et al. 1989), CANOCO has been applied to phytoplankton data only twice previously (Fangström and Willén 1987; Willén et al. 1990). The output as species and site "biplots" displayed along environmental gradients offers relatively straightforward interpretation and considerable potential for further application to phytoplankton data. Even at the rather coarse level of data input undertaken in this study (mostly genus level identifications) several clear associations of algal taxa with trophic state and acidification-related variables emerged.

The most significant finding however, was the existence of well-defined relationships between numbers of phytoplankton taxa and alkalinity for the 111-lake set and numbers of taxa and pH for the seven lake set. Along with the lack of a relationship between total phytoplankton biovolume and alkalinity, these findings are consistent with recent experimental work on whole lake acidification (Findlay and Kasian 1990), with several other regional studies of phytoplankton in lakes affected to various degrees by acidification (Almer et al. 1974; Dillon et al. 1979; Kwiatkowski and Roff 1976; Raddum et al. 1980; Hörnström and Ekström 1986) and with predictive models of species loss (Minns et al. 1990). While most of the previously published conclusions regarding loss of species richness with acidification have resulted from synoptic surveys, the seven lake set reported here is one of the few examples of a time series study (in this case, about 10 years) where phytoplankton response has been determined as a direct response to lake "deacidification". Alkalinity additions by whole lake liming operations have also achieved similar recoveries of phytoplankton species richness (Molot et al. 1990; Eriksson et al. 1983; Weatherley 1988); however, these responses have been measured in "artificially" recovered systems over short periods (1-3 years). Only in one other study, in Western Sweden where lakes have been subjected to decreased acid deposition, has "natural" recovery of the phytoplankton been documented (Morling and Willén 1990). Interestingly, in the Swedish study, evidence for recovery in their "Phase III" lakes was based on minor shifts in taxonomic composition, and with regard to acidified lakes, the authors concluded that "acidification did not markedly change the number and composition of the phytoplankton, which to some degree diverges from earlier results presented in the literature".

In our larger (111 lakes) data set, there were associations or subsets of lakes with highly similar phytoplankton community structure which may have been determined by water chemistry (groupings of low alkalinity lakes were distinguishable from other groupings of high alkalinity lakes). However, there were enough exceptions to this within the entire data set to preclude any generalization about an overall relationship between phytoplankton structure and lake alkalinity. This probably was a consequence of the lack of species identifications. For example, it is now well known that several species of *Mallomonas* are distinctly alkaliphilous, while several other species are acidophilous (Siver and Hamer 1990). By not identifying *Mallomonas* and other genera to the species level, we undoubtedly have lost some resolution in the phytoplankton composition-environmental gradient analysis.

The CCA analysis of the 111-lake set did not resolve phytoplankton associations responding to trophic state (total biovolume) changes from those responding to alkalinity changes because the directions of major influence of these variables in the ordination field were nearly identical. However, the seven lake set included Welcome lake, a reference lake with circum-neutral pH that experienced no change in acid neutralizing capacity. In Welcome Lake, 70% of the shifts in taxonomic composition were predictable on the basis of the nutrient/trophic status axes in the CANOCO analysis. This was substantiated by the observed increase in total phytoplankton biomass of 68% at Station 1 and 56% at Station 2 between the mid-1970s and the mid-1980s. Similarly, in Wavy Lake species richness closely followed total phytoplankton biovolume over the three year period of observation of all three sampling sites. In general, however, total biovolume was not a significant co-predictor of species richness for the entire seven lake data set ($n = 52$, all stations, all years), undoubtedly because of the overriding influence of the changes in alkalinity. In a multiple linear regression analysis including only alkalinity and biovolume as independent variables, alkalinity contributed more than 80% of the total multiple coefficient of determination ($R^2 = 0.710$).

Major changes in nutrient supply to Welcome Lake and Wavy Lake over the ten year period of observation were not measured and therefore cannot be inferred as the reason for phytoplankton biomass changes in these lakes. Trophic state may have been influenced by changes in grazing pressure from secondary producers which may have been influenced by changes in fish community structure or other environmental variables. The observed species richness increase in Welcome Lake has been tentatively explained on the basis of a total biovolume-species richness relationship. However, it is likely that metal concentrations declined (even though acidity did not change measurably) over the past decade, because Welcome Lake is within a geographic zone influenced by metal contributions from the Sudbury smelter (Keller and Pitblado 1986). For example, limited data suggest that surface water concentrations of Cu declined from about 3 μg/L to 1 μg/L between the mid 1970s and the mid 1980s (Keller and Yan 1991). Some of the increase in taxonomic richness in Welcome Lake may therefore have resulted from decreased metal stress. In Joe Lake, 77% of all taxonomic shifts in abundance were predictable on the basis of the CANOCO ordinations (the Al axis and the Alk/trophic status axes). But, because there was no evidence of a major change in trophic state (total phytoplankton biomass actually decreased slightly between the mid-1970s and the mid-1980s), the increase in phytoplankton species richness was most probably a direct response to the increase in pH from 5.6 to 6.3.

Damage to phytoplankton communities in acidified lakes through loss of species richness would appear to be reversible. These findings, together with the documented recoveries of other biotic groups in Sudbury area lakes (Keller et al. 1992), demonstrate that SO_2 emission controls and associated decreased acid deposition to lakes may lead eventually to restoration of aquatic communities, given adequate opportunities for dispersal and recolonization by aquatic organisms.

ACKNOWLEDGEMENTS

We thank Peggy Gale and Ron Griffiths for field assistance and Roger Pitblado and Tom Brown for data management. Norm Yan provided a thorough review and helpful comments on an earlier draft, and the editor (D.G. Cook) provided useful suggestions for rewording parts of the text.

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Table 1. Linear correlation co-efficients ("r" values) for biovolume and numbers of taxa of the dominant phytoplankton classes and total phytoplankton vs total phosphorus, alkalinity, aluminum and copper concentrations in the 111 lake set. Asterisks show significance at the 95% confidence level.

Biovolume (mm^3/L)	**Total P (µg/L)**	**TIP Alkalinity (mg/L)**		**Aluminum (µg/L)**	**COPPER (µg/L)**
		(entire range)[1]	**(-2 - 10 mg/L)**		
Cyanophyceae	0.232*	0.039	0.334*	-0.207	-0.166
Cyano. bloomers	0.208*	0.081	0.231*	-0.169	-0.072
Cyano. non-bloomers	0.176	0.008	0.286*	-0.165	-0.161
Dinophyceae	-0.086	-0.041	-0.085	-0.074	-0.058
Cryptophyceae	0.238*	0.338*	0.270*	-0.328*	0.159
Chrysophyceae	0.089	0.007	0.149	-0.175	0.009
Chlorophyceae	0.329*	0.251*	0.189	-0.236*	0.279*
Bacillariophyceae	0.291*	0.225*	0.454*	-0.302*	-0.001
Total phytoplankton	0.314*	0.237*	0.421*	-0.400*	0.011
NO. OF TAXA					
Cyanophyceae	0.194	0.061	0.450*	-0.539*	-0.250*
Dinophyceae	0.040	0.155	0.025	0.120	0.047
Cryptophyceae	0.227*	0.227*	0.463*	-0.608*	-0.116
Chrysophyceae	-0.008	-0.049	0.094	-0.232*	-0.109
Chlorophyceae	0.334*	0.148	0.362*	-0.350*	-0.037
Bacillariophyceae	0.311*	0.260*	0.553*	-0.492*	-0.008
Total	0.281*	0.176	0.457*	-0.480*	-0.101

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[1] Footnote: The entire alkalinity range (-2 - 32 mg/L) does not include Lake No. 173 (Shining Tree Lake) with an alkalinity of 94 mg/L.

Table 2. May-October average total phytoplankton biovolume and "average" lake pH (calculated from H^+ concentrations) in the seven Sudbury area lakes.

Lake		**Year**	**Biovolume (mm^3/L)**	**pH**	**Number of taxa**
Joe	Stn 1	1975	0.448	5.7	34
		1985	0.342	6.2	50
		1986	0.376	6.3	54
	Stn 2	1975	0.448	5.7	31
		1985	0.265	6.2	48
		1986	0.402	6.3	49
Laundrie	Stn 1	1975	0.254	4.9	25
		1976	0.283	4.8	34
		1985	0.339	5.5	47
		1986	0.256	5.6	54
	Stn 2	1975	0.223	4.9	26
		1976	0.529	4.9	33
		1985	0.300	5.4	41
		1986	0.310	5.6	55
	Stn 3	1975	0.304	5.1	29
		1976	0.630	5.1	20
		1985	0.294	6.0	48
		1986	0.424	6.0	51
Sans Chambre		1980	0.340	5.4	25
		1981	0.349	5.4	37
		1983	0.143	5.8	38
		1985	0.352	5.9	33
Swan		1977	0.867	4.0	20
		1982	0.567	4.8	23
		1983	0.727	5.0	20
		1984	1.089	5.1	23
		1985	0.808	5.2	25
		1986	1.257	5.7	23
Wavy	Stn 1	1974	0.066	4.4	19
		1985	0.441	4.8	27
		1986	0.252	4.7	22

Table 2. (continued)

Lake		Year	Biovolume (mm^3/L)	pH	Number of taxa
	Stn 2	1974	0.044	4.5	19
		1985	0.477	4.7	22
		1986	0.183	4.7	22
	Stn 3	1974	0.069	4.4	15
		1985	0.338	4.7	27
		1986	0.194	4.7	20
Welcome	Stn 1	1975	0.236	6.9	42
		1976	0.213	6.7	57
		1985	0.438	6.9	58
		1986	0.320	6.9	70
	Stn 2	1975	0.252	6.8	48
		1976	0.289	6.7	54
		1985	0.440	6.9	66
		1986	0.403	6.9	58
Whitepine		1980	0.498	5.5	33
		1981	0.295	5.7	25
		1982	0.376	5.8	36
		1983	0.356	5.8	45
		1984	0.307	5.8	43
		1985	0.338	5.8	50
		1986	0.143	5.9	38

Appendix I. List of lakes and locations sampled for phytoplankton. The numbers correspond to those used in Figures 4d, 5 and 7.

Lake Number	Lake Name	Latitude	Longitude
2	Windy	46°36′N	81°27′W
6	Skill	46°27′N	81°24′W
16	Raft	46°24′N	80°57′W
17	McFarlane	46°25′N	80°59′W
37	Kakakiwaganda	46°11′N	80°47′W
38	Magnetawan R.	45°44′N	80°23′W
39	Naiscoot	45°31′N	80°20′W
40	Round	45°31′N	80°08′W
41	Otter	45°17′N	79°58′W
42	Trout	45°32′N	80°10′W
45	Eagle	45°50′N	79°30′W
47	Shawanaga	45°34′N	79°59′W
50	Chiniguchi	46°57′N	80°42′W
54	Laura	46°53′N	80°38′W
56	Temagami	47°10′N	80°08′W
60	Lady Evelyn	47°20′N	80°10′W
65	Hammond	47°31′N	79°52′W
67	Yorston	47°03′N	80°32′W
68	Bassoon	46°13′N	81°23′W
69	Bear	46°12′N	81°27′W

Appendix I. (continued)

Lake Number	Lake Name	Latitude	Longitude
70	Threenarrows	46°05′N	81°27′W
71	Nellie	46°07′N	81°30′W
72	Elizabeth	46°15′N	81°38′W
75	Helen	46°07′N	81°34′W
77	Annie	46°11′N	81°08′W
79	O.S.A.	46°03′N	81°24′W
80	George	46°02′N	81°24′W
83	Margaret	46°17′N	81°27′W
86	Shoofly	47°13′N	81°24′W
87	Barnet	47°10′N	81°11′W
88	Welcome	47°13′N	81°02′W
92	Sunnywater	47°24′N	80°37′W
93	Laundrie	47°07′N	80°52′W
94	Florence	47°15′N	80°33′W
95	Mountain	47°39′N	80°14′W
101	Armstrong	46°32′N	81°33′W
113	Tyson	46°07′N	81°07′W
114	Bell	46°08′N	81°12′W
115	Bird	46°04′N	80°56′W
116	Broker	46°08′N	81°00′W

Appendix I. (continued)

Lake Number	Lake Name	Latitude	Longitude
117	Fraleck	46°55′N	80°53′W
118	Telfer	46°56′N	80°47′W
123	Frederick	47°02′N	80°44′W
125	Obushkong	47°42′N	80°48′W
126	Shack	47°30′N	80°37′W
127	Makobe	47°27′N	80°27′W
128	McKee	47°23′N	80°55′W
129	Solace	47°11′N	80°42′W
130	Alphretta	46°59′N	80°46′W
131	Sam Martin	46°53′N	80°48′W
132	Hutton	46°49′N	81°00′W
133	Morrison	44°52′N	79°27′W
134	Bigwind	45°03′N	79°03′W
136	Nine Mile	44°57′N	79°35′W
137	Skeleton	45°15′N	79°27′W
138	Bass	45°06′N	79°42′W
139	Blackwater	45°25′N	79°49′W
140	Horn	45°24′N	79°36′W
143	Klock	47°28′N	80°08′W
144	Wawashkesh	45°43′N	80°02′W

Appendix I. (continued)

Lake Number	Lake Name	Latitude	Longitude
145	Lahay	47°06′N	80°23′W
147	Erables	46°00′N	78°48′W
148	Biggar	45°57′N	78°55′W
149	La Muir	45°50′N	78°35′W
150	Proulx	45°46′N	78°24′W
152	Chateau	46°06′N	78°01′W
153	Foys	45°47′N	77°53′W
154	Brûlé	45°38′N	78°49′W
155	Buck	45°25′N	79°23′W
156	Tim	45°45′N	79°02′W
157	Bernard	45°45′N	79°23′W
159	Red Pine	45°12′N	78°42′W
160	Smoke	45°31′N	78°41′W
161	Louisa	45°28′N	78°29′W
162	Hunter	46°21′N	81°48′W
173	Shining Tree	47°33′N	81°04′W
175	Little Burwash	47°06′N	81°07′W
177	Mary	45°15′N	79°15′W
181	Whitepine	47°23′N	80°38′W
185	Chief	47°29′N	80°06′W

Appendix I. (continued)

Lake Number	Lake Name	Latitude	Longitude
186	Lady Sydney	47°24'N	80°12'W
187	Trethewey	47°26'N	80°30'W
188	Sugar	47°21'N	80°06'W
190	Banks	47°30'N	80°20'W
193	Lepha	47°32'N	80°03'W
195	Anvil	47°25'N	80°16'W
196	Mendelssohn	47°32'N	80°12'W
197	Wabun	47°25'N	80°36'W
198	Anima Nipissing	47°14'N	79°57'W
200	Cooke	47°36'N	80°21'W
203	Mowat	46°52'N	80°57'W
204	Kasakanta	47°27'N	81°09'W
206	Lang	46°10'N	81°40'W
207	Halifax	46°14'N	81°01'W
209	Burwash	47°07'N	81°03'W
211	Manitouwabing	45°29'N	79°54'W
214	David	46°08'N	81°18'W
215	Johnnie	46°07'N	81°14'W
219	Mahzenazing	46°03'N	81°11'W
224	Killarney	46°04'N	81°22'W

Appendix I. (continued)

Lake Number	Lake Name	Latitude	Longitude
225	Bowland	47°05′N	80°50′W
236	Bluesucker	47°10′N	80°37′W
237	Dougherty	47°01′N	80°40′W
239	Carlyle	46°04′N	81°17′W
241	Linger	47°05′N	80°30′W
242	Little Laundrie	47°07′N	80°47′W
244	Seagram	47°06′N	80°32′W
246	Parkin	46°53′N	80°52′W
249	Pilgrim	47°11′N	80°41′W
250	Rome	47°00′N	81°19′W

Appendix 2. List of taxa identified in summer phytoplankton samples. The numbers correspond to those used in Figure 6.

1	*Anabaena*
2	*Aphanizomenon*
3	*Aphanocapsa*
4	*Aphanothece*
5	*Chroococcus*
6	*Coelosphaerium*
7	*Gomphosphaeria*
8	*Lyngbya*
9	*Merismopedia*
10	*Microcystis*
11	*Oscillatoria*
12	*Rhabdoderma*
13	*Ceratium*
14	*Gymnodinium*
15	*Peridinium*
16	*Peridinium inconspicuum*
17	*Peridinium limbatum*
18	*Peridinium wisconsinense*
19	*Urococcus*
20	*Unidentified armoured dinophyceae*
21	*Unidentified dinophyceae*
22	*Unidentified naked dinophyceae*

Appendix 2. (continued)

23	*Bicosoeca*
24	*Bitrichia*
25	*Chromulina*
26	*Chromulina erkensis*
27	*Chrysochromulina*
28	*Chrysochromulina breviturrita*
29	*Chrysochromulina parva*
30	*Chrysococcus*
31	*Chrysolykos*
32	*Chrysolykos cysts*
33	*Chrysolykos planctonicus*
34	*Chrysolykos Skujai*
35	*Chrysosphaerella*
36	*Chrysosphaerella coronacircumspina*
37	*Chrysosphaerella longispina*
38	*Dinobryon*
39	*Dinobryon cysts*
40	*Kephyrion*
41	*Mallomonas*
42	*Mallomonas a*
43	*Mallomonas b*
44	*Ochromonas*

Appendix 2. (continued)

45	*Salpingoeca*
46	*Spiniferomonas*
47	*Synura*
48	*Uroglena*
49	*Uroglenopsis*
50	*Unidentified banana chrysophyte*
51	*Unidentified chrysomonad*
52	*Unidentified chrysophyte*
53	*Unidentified chrysophycean cysts*
54	*Cryptomonas*
55	*Cryptomonas a*
56	*Cryptomonas b*
57	*Katablepharis*
58	*Rhodomonas*
59	*Euglena*
60	*Phacus*
61	*Trachelomonas*
62	*Ankistrodesmus*
63	*Arthrodesmus*
64	*Bambusina*
65	*Botryococcus*
66	*Carteria*

Appendix 2. (continued)

67 *Chlamydomonas*

68 *Chodatella*

69 *Closterium*

70 *Coelastrum*

71 *Cosmarium*

72 *Crucigenia*

73 *Dictyosphaerium*

74 *Elakatothrix*

75 *Euastrum*

76 *Eudorina*

77 *Franceia*

78 *Gloeocystis*

79 *Kirchneriella*

80 *Micrasterias*

81 *Monoraphidium*

82 *Mougeotia*

83 *Nephrocytium*

84 *Oedogonium*

85 *Oocystis*

86 *Paramastix*

87 *Pediastrum*

88 *Pedinomonas*

Appendix 2. (continued)

89	*Planctonema*
90	*Quadrigula*
91	*Scenedesmus*
92	*Schroederia*
93	*Spondylosium*
94	*Staurastrum*
95	*Staurodesmus*
96	*Teilingia*
97	*Tetraëdron*
98	*Tetrastrum*
99	*Ulothrix*
100	*Xanthidium*
101	*Unidentified chlorophyceae*
102	*Unidentified chlorophycean cysts*
103	*Achnanthes*
104	*Asterionella*
105	*Cyclotella*
106	*Cymbella*
107	*Eunotia*
108	*Fragilaria*
109	*Gomphonema*
110	*Melosira*

Appendix 2. (continued)

111 Navicula

112 Nitzschia

113 Rhizosolenia

114 Rhizosolenia chloroplasts

115 Stauroneis

116 Stephanodiscus

117 Surirella

118 Synedra

119 Tabellaria

120 Tabellaria fenestrata

121 Tabellaria flocculosa

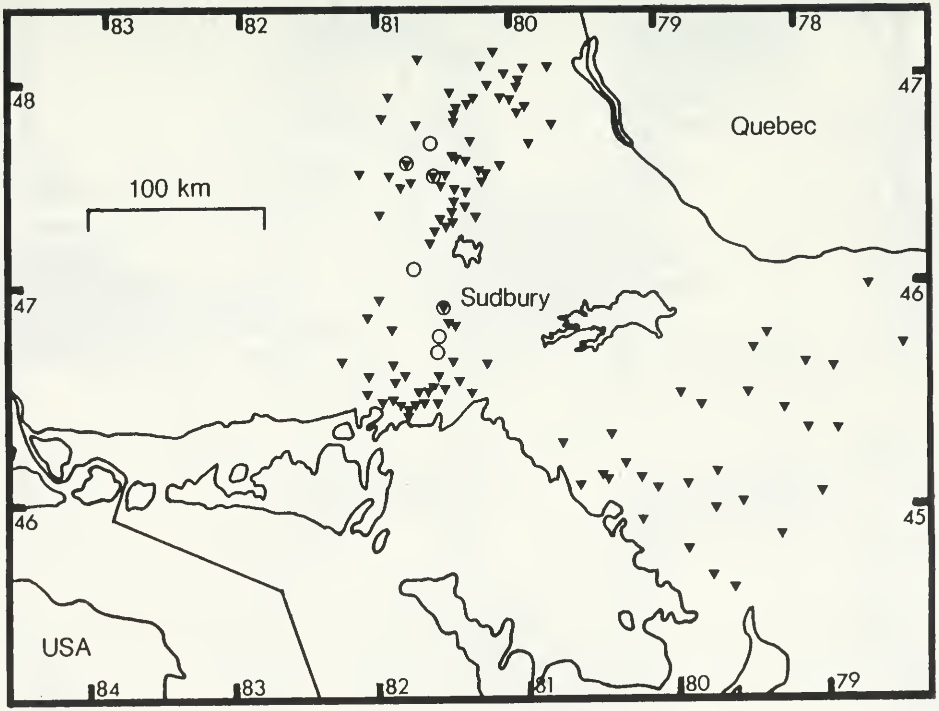


Figure 1: Map of the study area showing the location of the lakes. The larger lake set (111 lakes) is marked with solid triangles, the smaller lake set (7 lakes) with open circles. Three lakes are common to both data sets.

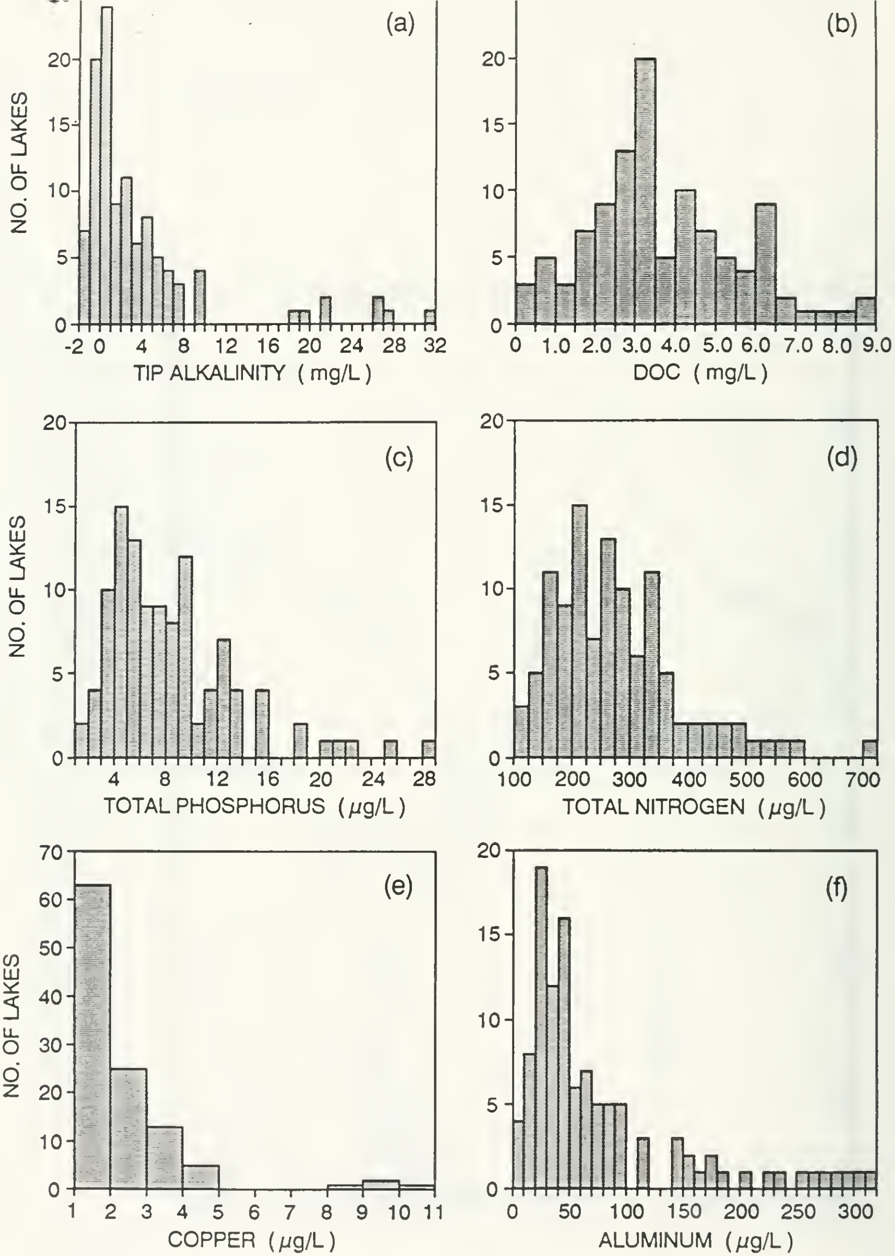


Figure 2: Frequency distributions for ranges of chemical variables in the 111 lake set: (a) total inflection point alkalinity (note: does not include one outlier at 94 mg/L); (b) dissolved organic carbon; (c) total phosphorus; (d) total nitrogen; (e) copper; (f) aluminum.

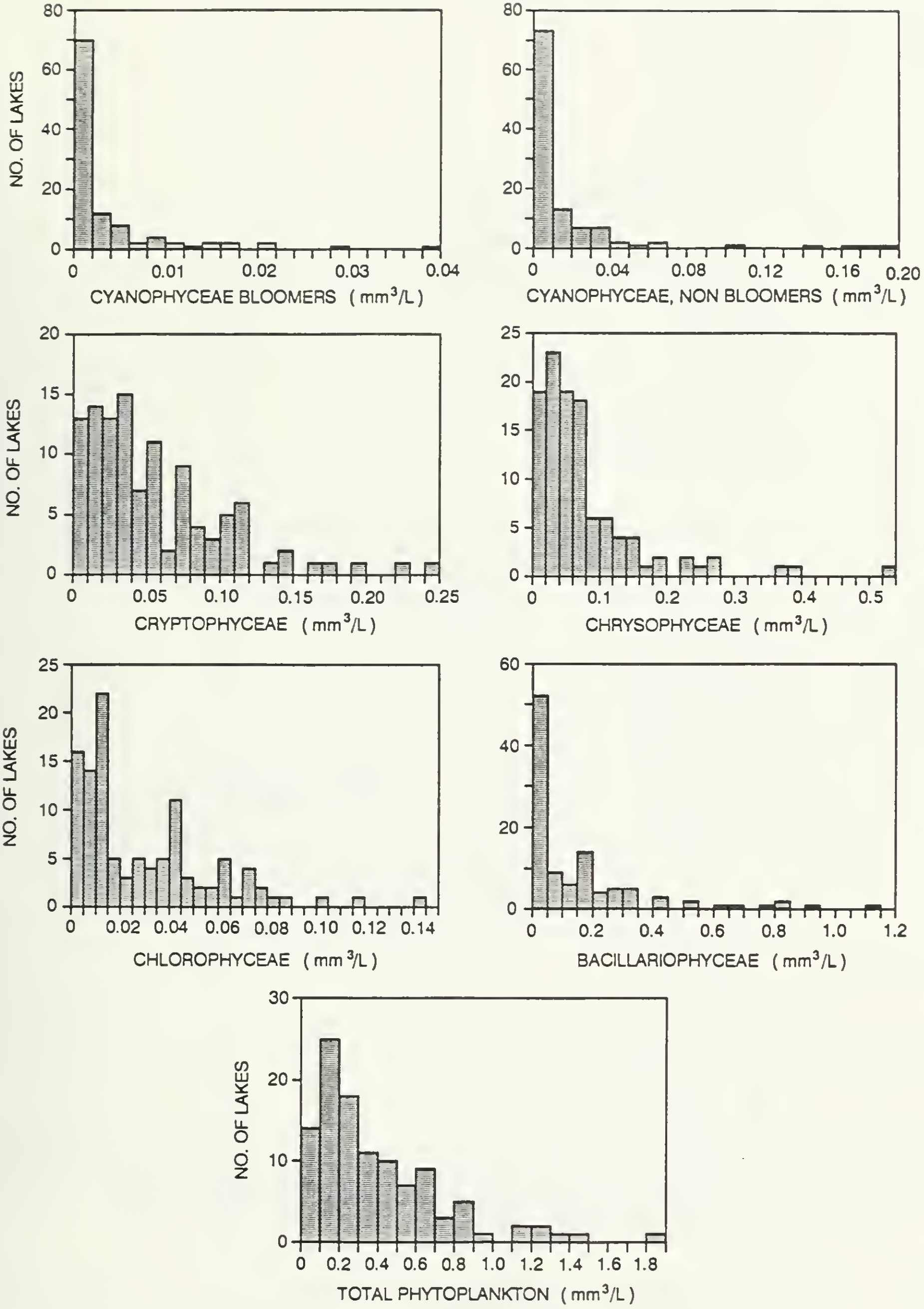


Figure 3: Frequency distributions for density (biovolume) ranges of total phytoplankton and the dominant classes in the 111 lake set. Note: blue-green "non-bloomers" were predominantly species of *Merismopedia*, *Aphanothece*, *Chroococcus*, *Rhabdoderma* and *Aphanocapsa*, while "bloomers" were mainly species of *Anabaena*, *Aphanizomenon*, *Lyngbya*, *Oscillatoria*, *Microcystis*, *Coelosphaerium* and *Gomphosphaeria*.

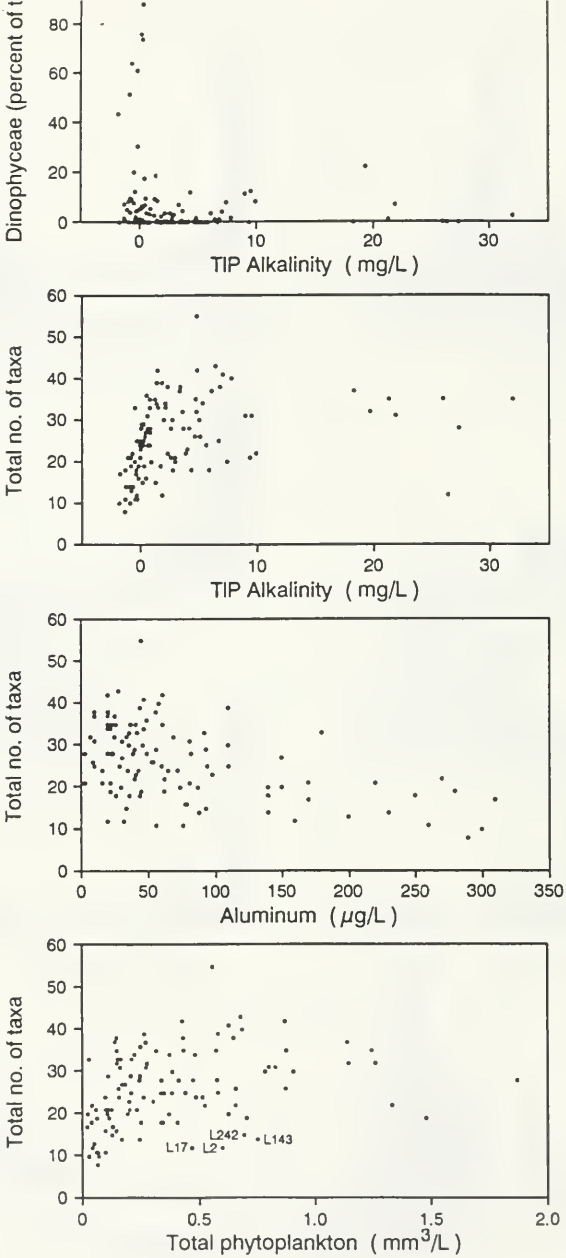


Figure 4: Relationships among phytoplankton and alkalinity or Al in the 111 lake set: a) Dinophyceae (as a percentage of total phytoplankton biovolume) and lake alkalinity; b) total number of phytoplankton taxa and lake alkalinity; c) total number of phytoplankton taxa and total aluminum concentration; and d) total phytoplankton biovolume and the total number of phytoplankton taxa ($r = 0.303$). A few lakes may be outliers for reasons relating to atypical combinations of physico-chemical features, e.g. L. 17 was extremely high in total dissolved salts (cond. = 264 µS; Cl^- = 44 mg/L); L. 143 was shallow (7m) and high in Al (100 µg/L).

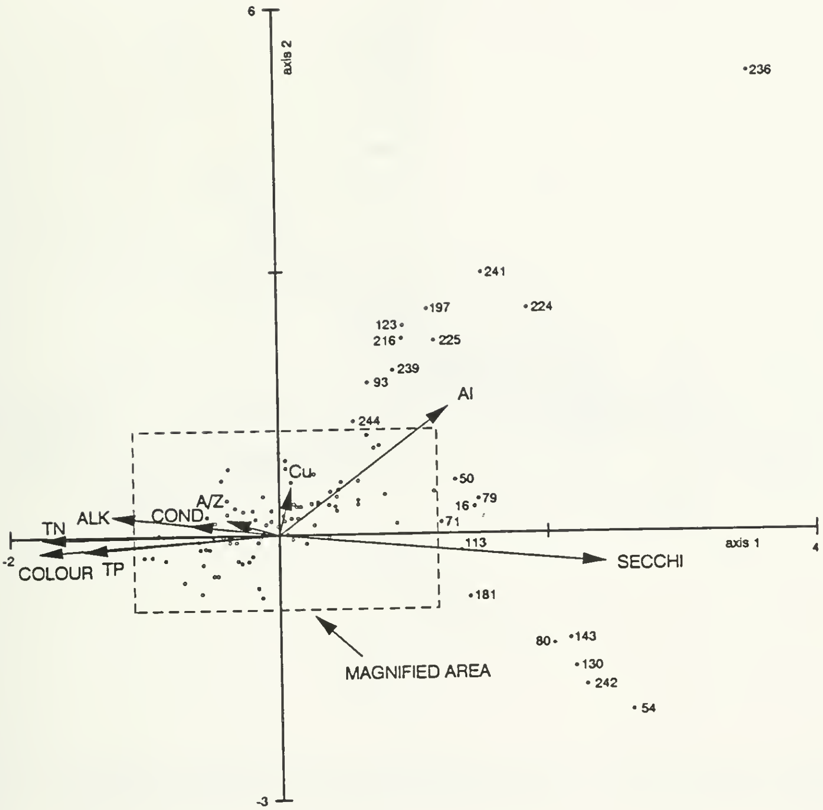


Figure 5a: Location of lakes within the CCA (canonical correspondence analysis) ordination field with axes defined by major environmental variables. (A/Z = ratio of lake area to maximum depth; ALK = alkalinity; COND = specific conductance (25°C); TN = total nitrogen; TP = total phosphorus). Lake numbers are keyed in Appendix I.

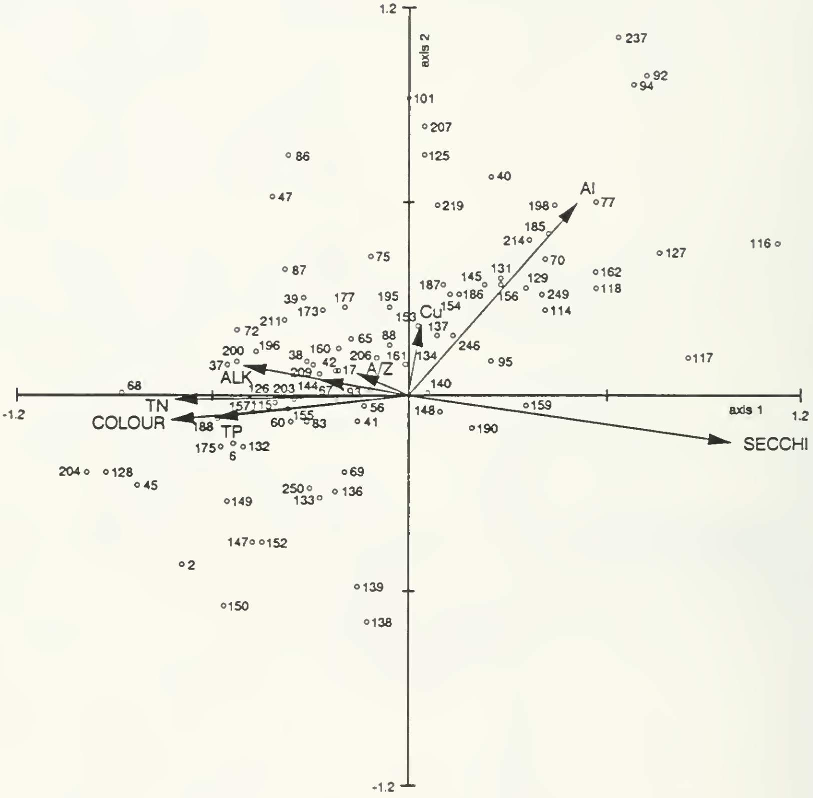


Figure 5b: Magnified area showing lake locations near the origin.

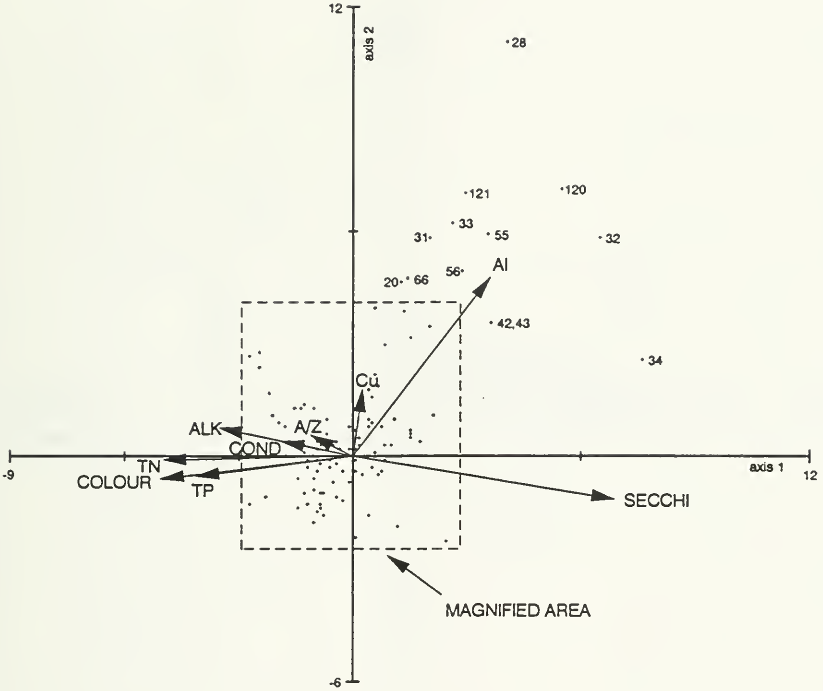


Figure 6a: Location of phytoplankton taxa within the CCA ordination field with axes defined by major environmental variables. Taxon numbers are keyed in Appendix 2.

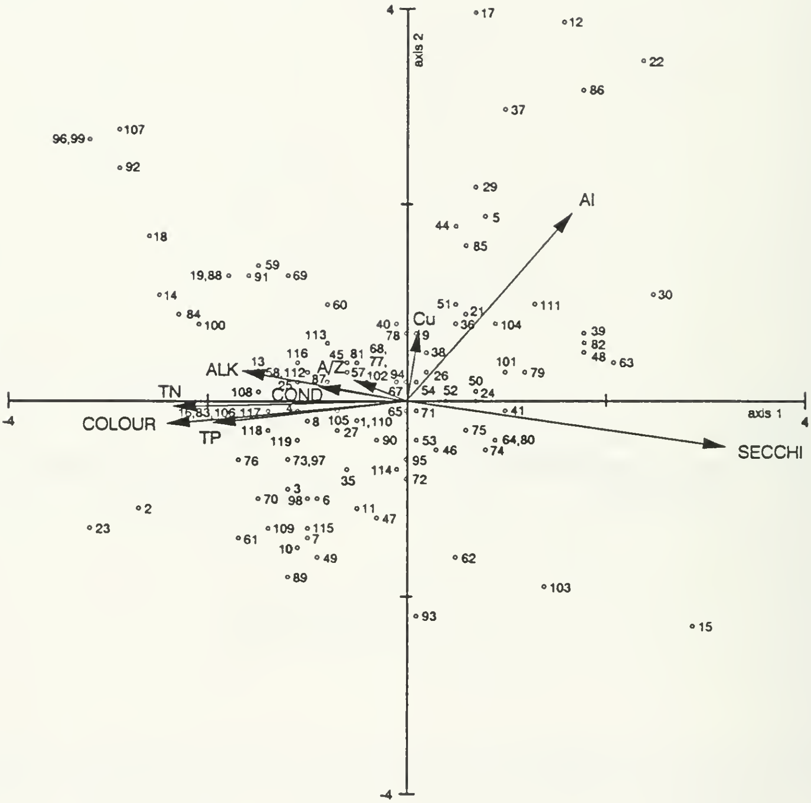


Figure 6b: Magnified area showing taxon locations near the origin.

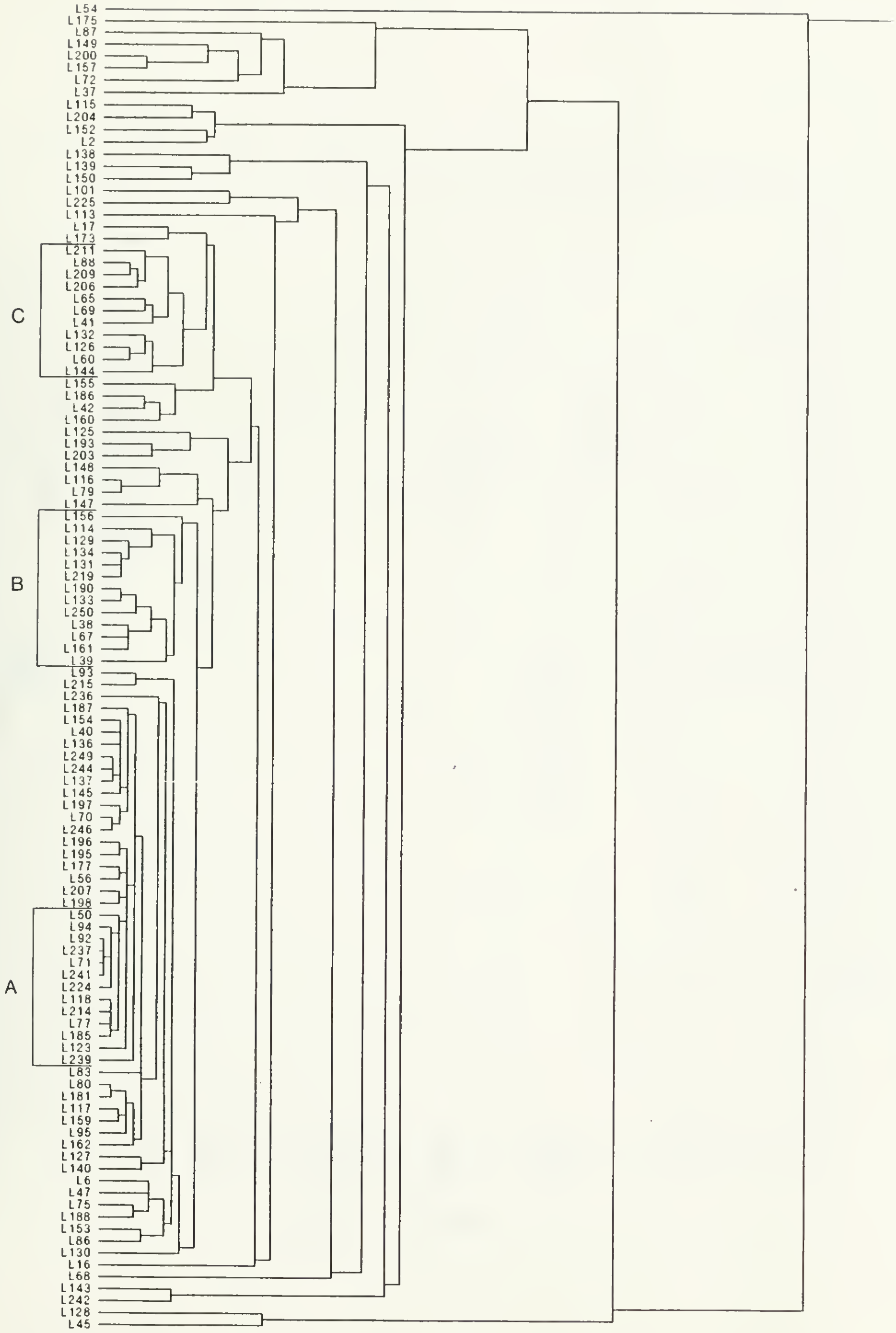


Figure 7: Dendrogram (complete linkage method) of lakes based on phytoplankton dissimilarities calculated for all possible pairs of lakes (lakes are identified in Appendix I). See text for explanation of A, B and C.

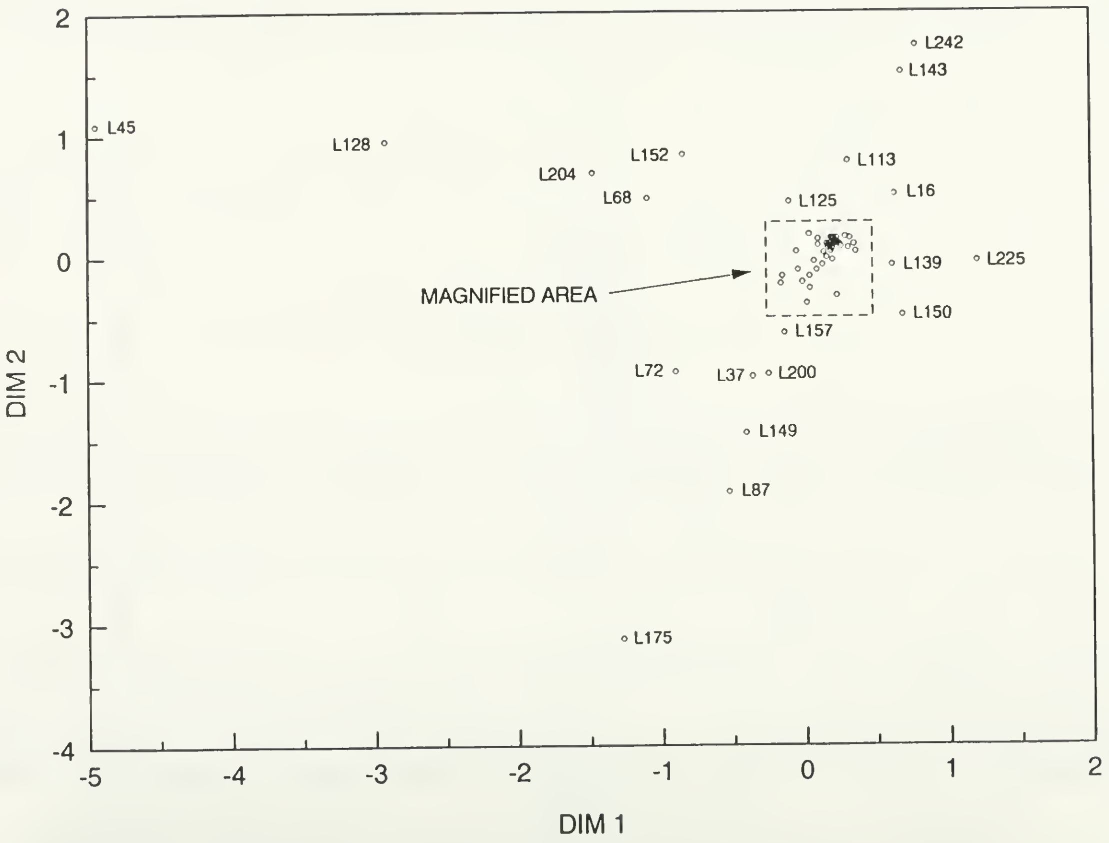


Figure 8a: Locations of lakes within a two dimensional MDS ordination field based on measures of dissimilarity of the phytoplankton communities calculated for all possible pairs of lakes.

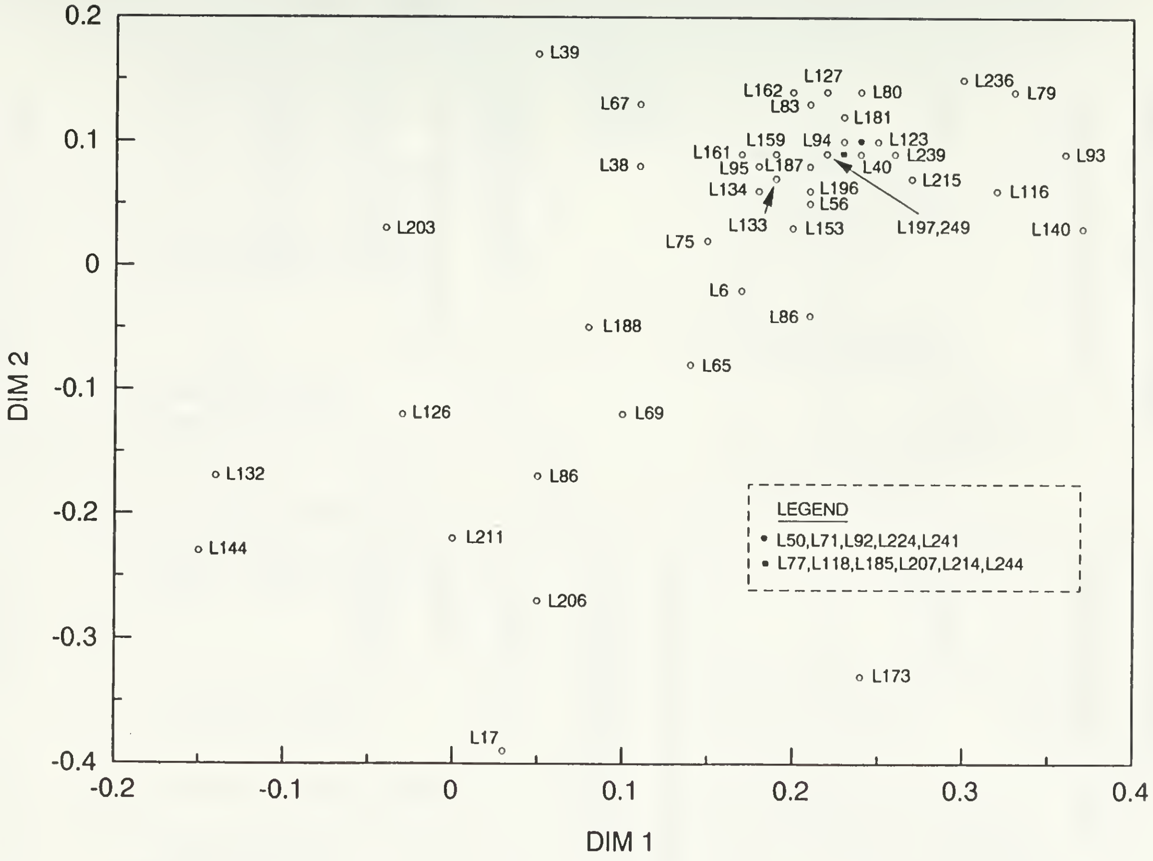


Figure 8b: Detailed placement of lakes within the ordination field of the magnified area.

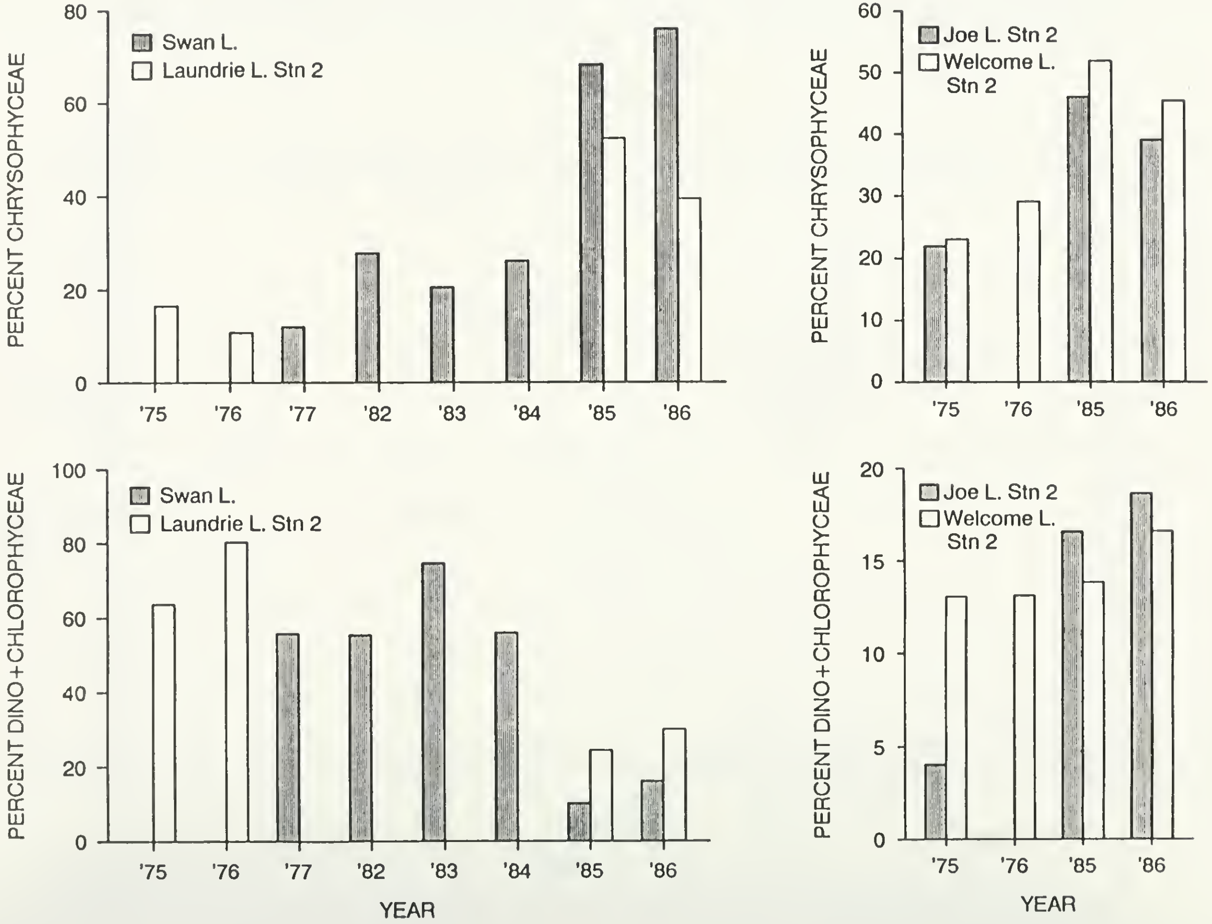
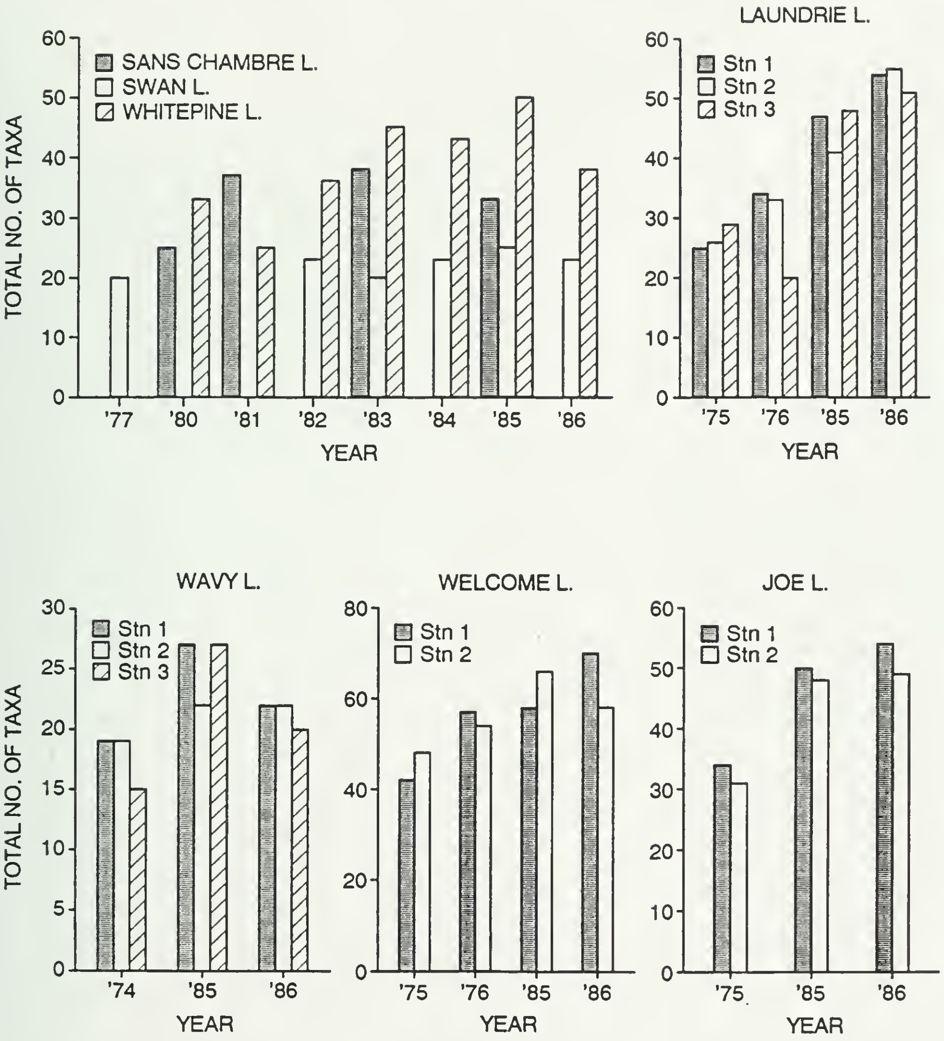


Figure 9: Changes in the relative contributions of Chrysophyceae and Dinophyceae + Chlorophyceae in Swan Lake, Laundrie Lake, Joe Lake and Welcome Lake between 1975 and 1986.



LAUNDRIE L.

WAVY L.

WELCOME L.

JOE L.

Figure 10: Changes in the total numbers of phytoplankton taxa in seven Sudbury area lakes over approximately a 10 year period.

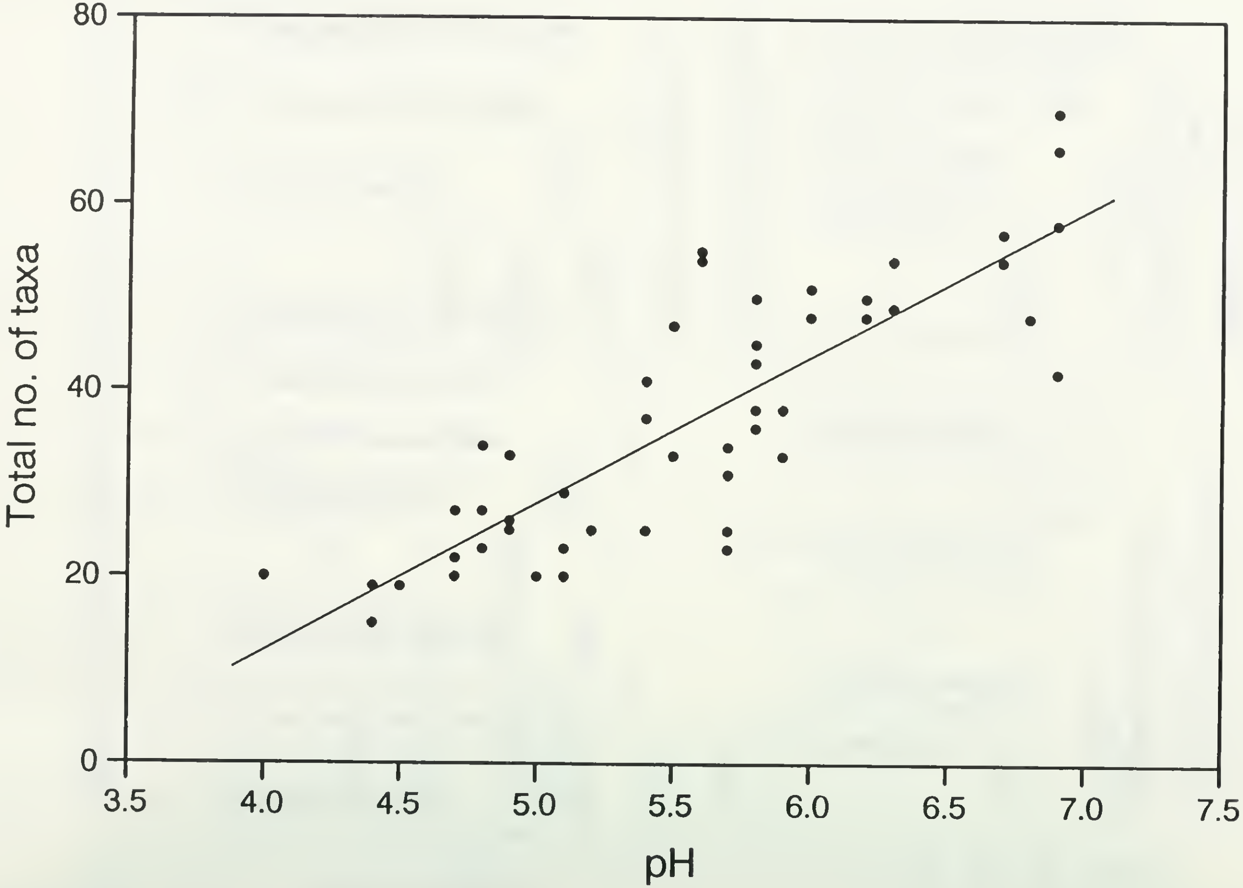


Figure 11: Relationship between lake pH and total number of phytoplankton taxa in the seven Subdury area lakes ($R^2 = 0.731$, n = 52).